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Effects of seasonality, trophic state and landscape properties on CO_2 saturation in low-latitude lakes and reservoirs

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HIGHLIGHTS

- CO_2 supersaturation is prevalent in eutrophic low-latitude fresh waters
- The pCO_2 was significantly higher in these lakes than at higher latitudes
- Rainy season resulted in high pCO_2 in low-latitude freshwater systems
- pCO_2 increased as eutrophication decreased with higher water volume
- Land-use types directly affected trophic state but not water pCO_2

GRAPHICAL ABSTRACT

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ABSTRACT

The role of tropical lakes and reservoirs in the global carbon cycle has received increasing attention in the past decade, but our understanding of its variability is still limited. The metabolism of tropical systems may differ profoundly from temperate systems due to the higher temperatures and wider variations in precipitation. Here, we investigated the spatial and temporal patterns of the variability in the partial pressure of carbon dioxide (pCO_2) and its drivers in a set of 102 low-latitude lakes and reservoirs that encompass wide gradients of precipitation, productivity and landscape properties (lake area, perimeter-to-area ratio, catchment size, catchment area-to-lake area ratio, and types of catchment land use). We used multiple regressions and structural equation modeling (SEM) to determine the direct and indirect effects of the main in-lake variables and landscape properties on the water pCO_2 variance. We found that these systems were mostly supersaturated with CO_2 (92% spatially and 72% seasonally) regardless of their trophic status and landscape properties. The pCO_2 values (9–40,020 μatm) were within the range found in tropical ecosystems, and higher ($p < 0.005$) than pCO_2 values recorded from high-latitude ecosystems. Water volume had a negative effect on the trophic state ($r = -0.63$), which mediated a positive indirect effect on pCO_2 ($r = 0.4$), representing an important negative feedback in the context of climate change-driven reduction in precipitation. Our results demonstrated that precipitation drives the pCO_2 seasonal

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variability, with significantly higher pCO_2 during the rainy season ($F = 16.67$; $p < 0.001$), due to two potential main mechanisms: (1) phytoplankton dilution and (2) increasing inputs of terrestrial CO_2 from the catchment. We conclude that at low latitudes, precipitation is a major climatic driver of pCO_2 variability by influencing volume variations and linking lentic ecosystems to their catchments.

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1. Introduction

Inland aquatic ecosystems play a central role in the global carbon (C) cycle (Tranvik et al., 2018), because they receive large amounts of organic matter (OM) from catchment areas and can either process (decompose) and emit carbon to the atmosphere (for instance, as carbon dioxide [CO_2] and methane [CH_4]) or bury this organic matter in the sediments (e.g. Richey et al., 2002; Tranvik et al., 2009; Kosten et al., 2010; Bastviken et al., 2011; Chen et al., 2011; Knoll et al., 2013). Most lakes in the world are small (<1 km^2; Downing et al., 2006), but emit as much as 15% and 40% of all CO_2 and CH_4, respectively, although lakes and ponds cover only 8.6% of the world land surface area (Holgerson and Raymond, 2016; Ollivier et al., 2018).

Photosynthesis and respiration are central processes in aquatic C cycling (Dodds and Cole, 2007). Primary producers incorporate massive amounts of CO_2 into OM (Williamson et al., 2009), drawing down the water CO_2 content. Conversely, respiration by both heterotrophic and autotrophic organisms releases CO_2 back into the water (Cole et al., 1994; Jonsson et al., 2001). Both processes are directly affected by temperature and nutrient (e.g. nitrogen [N] and phosphorus [P]) availability (see Dodds and Cole, 2007). Hydrologically driven inputs of inorganic C from the catchment (Weyhenmeyer et al., 2015; Wilkinson et al., 2016) and carbonate precipitation may also affect CO_2 saturation (Nõges et al., 2016; Stets et al., 2017). These processes are sensitive to large-scale climate-related factors such as variations in temperature (Sand-Jensen and Staehr, 2007; Marotta et al., 2009a) and precipitation (Sobek et al., 2005), and also to physical, biological and anthropogenic properties of the landscape surrounding aquatic systems and their catchments, such as topography, productivity, land use, area, and morphometry (Vanni et al., 2005; Ferland et al., 2012; Maberly et al., 2012; Staehr et al., 2012). Depending on the relative importance of these factors, aquatic ecosystems may function either as net sources of CO_2 to the atmosphere (net efflux) when the water is supersaturated with CO_2 with respect to the atmosphere, or as sinks of CO_2 from the atmosphere (net influx) when the water is CO_2-undersaturated (Tranvik et al., 2009).

The interaction between precipitation and land use in a drainage basin may impact the amount and composition of terrestrial OM and nutrient input to aquatic ecosystems (Vanni et al., 2005, 2011). This incoming terrestrial material fuels aquatic respiration, thereby increasing CO_2 emissions (Karlsson et al., 2007; Lapierre et al., 2013), while incoming nutrients stimulate both primary production and respiration (Carpenter et al., 1998; Bergström et al., 2008; Vanni et al., 2011). Therefore, the types of land use in catchments may ultimately affect C budgets (Knoll et al., 2013). For instance, well-preserved forest landscapes would input terrestrially derived organic and inorganic C, as well as decreasing the amount of key nutrients (nitrogen and/or phosphorus) entering water bodies, preventing eutrophication, and then supporting high water CO_2 levels (Butman and Raymond, 2011; Maberly et al., 2012; Knoll et al., 2013). Conversely, conversion of forests to agricultural systems usually leads to immediate soil C losses (Don et al., 2011), which increases the amounts of CO_2 in the water (Drake et al., 2017), but also increases nutrient input to aquatic ecosystems (Le Moal et al., 2019), which can stimulate primary production and C sequestration (Knoll et al., 2013; Pacheco et al., 2014). Whether conversion of catchment areas to agriculture causes a net increase or decrease of CO_2 concentration in water bodies is still not clear (Bodmer et al., 2016; Borges et al., 2018; Ollivier et al., 2018).

Most tropical inland waters show persistent CO_2 supersaturation across space and time (Marotta et al., 2009b, 2010; Roland et al., 2010), probably deriving from year-round high temperatures that cause an imbalance between respiration and production processes (Yvon-Durocher et al., 2010; Amado et al., 2013; Kraemer et al., 2017). Despite the increasing knowledge of C cycling in tropical lakes and reservoirs (e.g. Borges et al., 2015; Almeida et al., 2016; Kosten et al., 2018), not much is known about low-latitude ecosystems, especially in different climates (from near-coastal humid to inland semi-arid regions) and productivity gradients (from oligotrophic to hypereutrophic). For instance, northeastern Brazil (latitudes 4° to 6° S) has high temperatures year round and is a transition zone from coastal humid (approx. 1200 mm annual precipitation) (INMET, 2017) to semi-arid (from 400 to 800 mm annual precipitation) climates (Barbosa et al., 2012). These climate conditions create a strong gradient of residence time and trophic state across the aquatic ecosystems, i.e. higher nutrient concentrations in the semi-arid than in the coastal humid zone (Brasil et al., 2016; They et al., 2017; Menezes et al., 2018), which affects ecosystem processes such as primary production and decomposition (Dodds and Cole, 2007). The types of land use also change across this precipitation gradient, shifting between urban, agricultural, humid forest and Caatinga dry forest areas.

Here, we investigated the spatial and temporal patterns in the variability of pCO_2 and its drivers in 102 low-latitude lakes and reservoirs that encompass wide gradients of precipitation (climate variable), productivity (from oligotrophic to hypereutrophic), and landscape properties (lake area, lake perimeter-to-area ratio, catchment size, catchment area-to-lake area ratio, soil organic C (SOC) content and types of catchment land use). Our aims were (1) to determine the direct and indirect effects of the main internal and external variables driving pCO_2 variance; and (2) to determine the effects of precipitation on pCO_2 spatial and seasonal variability in a representative subset of these low-latitude systems. We hypothesized that most systems are supersaturated with CO_2 due to the year-round high temperatures in low latitudes, which stimulate ecosystem respiration more than net ecosystem production. However, within the general CO_2 supersaturation pattern across systems, we also expected to find (a) a high spatial variation in pCO_2 driven by differences in precipitation and catchment properties; and (b) wide seasonal variability, with higher CO_2 supersaturation during the rainy season, as a result of increasing water volume and, in turn, phytoplankton dilution, and a higher input of allochthonous organic and inorganic C.

2. Materials and methods

2.1. Study area and sampling design

We used two complementary approaches to evaluate the spatial and temporal variations of pCO_2 across aquatic ecosystems in the study area. First, we used a spatial snapshot approach including 102 aquatic ecosystems (32 lakes and 70 reservoirs) sampled in September 2012 (dry season) in an area of around 29,891 km^2 covering 14 (of 16 in total) watersheds of Rio Grande do Norte State in northeastern Brazil (Fig. 1). The perennial systems were chosen according to differences in climate (precipitation), trophic state and landscape properties (lake perimeter-to-area ratio, catchment area, and land use) (Fig. 2; mean limnological variables shown in Table S1). Most systems are shallow (90% have depths <4.00 m) and have small surface areas (86% cover <1 km^2, maximum area = 13.3 km^2). Sampling was conducted between

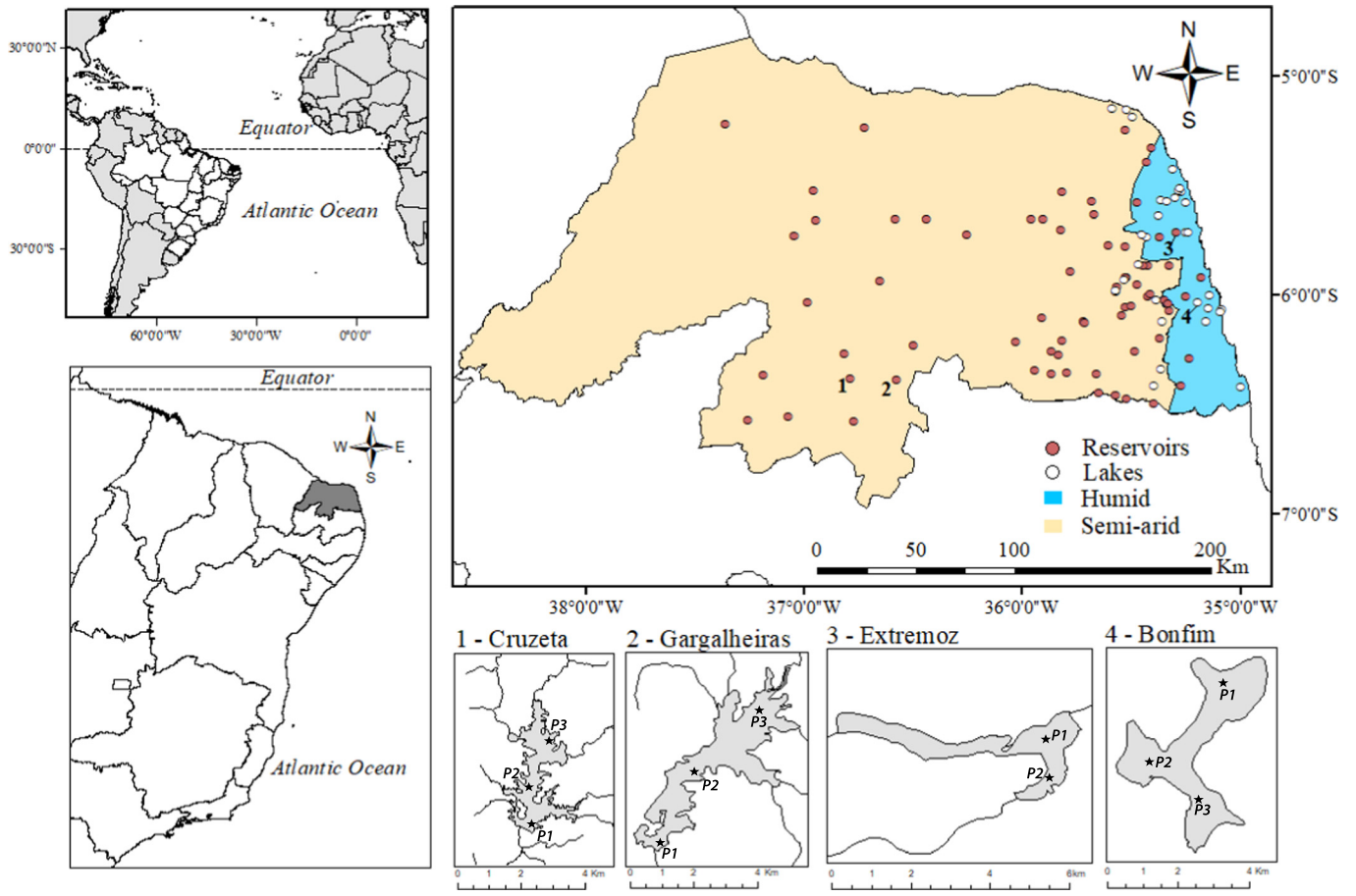

Fig. 1. Map of Rio Grande do Norte State, Brazil, showing the geographical locations of the 102 aquatic ecosystems sampled in this study. The four systems (Gargalheiras, Cruzeta, Extremoz and Bonfim) investigated seasonally are numbered in the lower part of the map. The black stars indicate the sampling stations (P1, P2 and P3) within each of these systems (see Table S1 for coordinates). This map was built using ArcGis 10.5.1 (ESRI, 2017).

06:00 h and 12:00 h (in 54 systems) and between 13:00 h and 17:00 h (in 48 systems). Standardizing the sampling time was not feasible because of the wide geographical distribution of the ecosystems (up to 3 systems were sampled in a day).

About 33% of the ecosystems are located in a semi-arid region (BSh climate, Köppen classification), and 67% are in the coastal region with a sub-humid and humid climate (BSh climate, Köppen classification). The semi-arid systems are all (100%) reservoirs, whereas the coastal systems are reservoirs (54%) and natural lakes (46%). The semi-arid reservoirs are located on shallow, low-permeable soils that prevent groundwater accumulation (Menezes et al., 2018), while the coastal lakes are located in sand dunes and are mostly supplied by groundwater (Menezes et al., 2018). These semi-arid reservoirs were constructed to store water by damming rivers, and therefore they generally have larger catchment area-to-lake area ratios than the coastal waterbodies. They also have a lower inflow water-to-evaporation ratio, and in turn, higher nutrient concentrations and phytoplankton biomass than the coastal lakes (They et al., 2017; Menezes et al., 2018).

Second, we employed a temporal approach aimed at capturing the seasonal variability of these systems, using a small subset ($n = 4$) of the 102 systems included in the spatial dataset (Fig. 1). In total we conducted 152 samplings in these four systems (Fig. 2; mean ± standard deviation of limnological variables shown in Table S2). Two systems are semi-arid eutrophic reservoirs (Gargalheiras and Cruzeta reservoirs), one is a sub-humid mesotrophic reservoir (Extremoz Reservoir) and one is a humid oligotrophic coastal lake (Bonfim Lake) (Table 1). Gargalheiras and Cruzeta reservoirs are in the Piranhas-Açu watershed (Fig. 1). They were sampled monthly from December 2010 to January 2012; during this period, the rainy season extended from December 2010 through July 2011 and the dry season from August 2011 through January 2012 (Fig. S1). Both reservoirs were constructed to store water, and therefore have no water outflow unless the water level rises above the dam, which occurred from May through July 2011 in Gargalheiras and from April through July 2011 in Cruzeta (Fig. S1). Three sampling sites were selected in each semi-arid reservoir (Fig. 1; see coordinates in Table S3).

Extremoz Reservoir, located in a sub-humid climate area in the Rio Doce watershed, and Bonfim Lake, located in a humid climate area in the eastern coastal watershed (Fig. 1), were also sampled monthly from July 2012 through July 2013 and from September 2014 through October 2015, respectively. For Extremoz Reservoir, the rainy season extended from April through July 2013 (besides July 2012) and the dry season from August 2012 through March 2013 (Fig. S1). We did not observe a strong seasonality with well-marked rainy and dry seasons in the area of Bonfim Lake (Fig. S1). Three sampling sites were selected in Bonfim Lake and two in Extremoz Reservoir (Fig. 1; see coordinates in Table S3). Sampling was conducted at around 10:00 h in Gargalheiras, Extremoz and Bonfim and at 13:00 h in Cruzeta.

2.2. Sample collection and field measurements

Water samples for measurements of nutrients and chlorophyll-*a* (chl-*a*) were collected with a Van Dorn bottle at the subsurface of the central limnetic zone of all 102 aquatic ecosystems and poured into 500-mL polyethylene dark bottles. At each sampling station, Secchi disc depth and maximum depth (Z_{max}) were measured. Dissolved oxygen and temperature were measured in situ with a portable digital probe (Instrutherm MO-900). Water samples for pH and alkalinity determination were carefully collected (avoiding turbulence and bubbles)

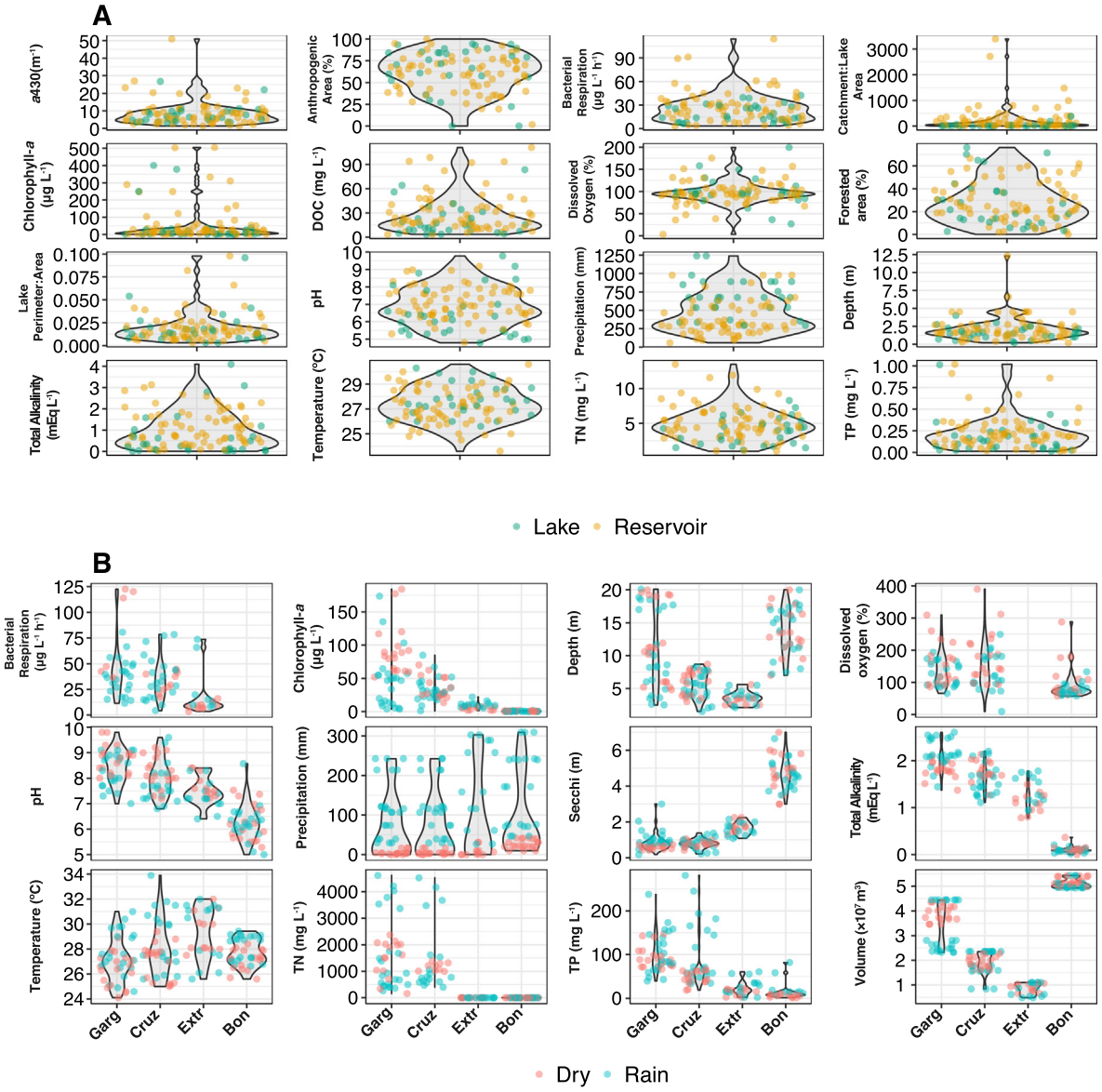

Fig. 2. Violin plots describing the variability of the main variables in the (A) spatial and (B) seasonal datasets. Each point represents an observation. The violin plot outlines illustrate kernel probability density, and the width of the shaded area represents the data distribution. Mean values and standard deviations of these variables are available in the Supplementary Material (Tables S1 and S2).

at the subsurface, using a 100-mL polyethylene bottle pre-rinsed with acid and distilled water, with no internal headspace. These bottles were kept in the dark at ambient temperature for approximately 10 min, and the analysis was performed on the shore of each ecosystem immediately after sampling (ca. 10 min; Benchtop pH Meter, MS Tecnopon® 210 MPa). Temperature, pH and alkalinity data were used for subsequent calculation of pCO_2, as described below. Precipitation data were acquired for each ecosystem from the nearest weather station (Source: INMET – Instituto Nacional de Meteorologia). For the spatial dataset, we used the cumulative yearly (from January 2012 through September 2012) precipitation up to the sampling date that marked the beginning of the dry period in the region. For the seasonal dataset, we used the cumulative monthly precipitation.

Table 1
Landscape properties and hydrological characteristics of the four aquatic ecosystems of the seasonal dataset. *Source: IGARN – Instituto de Gestão de Águas do Rio Grande do Norte.

	Semi-arid		Sub-humid/humid	
	Gargalheiras	Cruzeta	Extremoz	Bonfim
Catchment area (km²)	2114.74	995.95	325.85	12.55
Lake size (km²)	7.62	6.07	4.65	7.25
Perimeter (m)	35,300	38,977	21,939	22,692
Maximum volume* (m³)	44,421,480	23,545,745	11,019,525	84,268,200
Land cover				
Forest (%)	22.73	44.05	50.45	14.22
Grassland (%)	32.10	20.16	3.74	0.77
Agriculture & pasture (%)	42.4	35.13	44.36	81.82
Urban (%)	1.75	0.18	1.43	2.13
Anthropogenic (%)	44.2	35.3	45.8	2.13

2.3. Laboratory analysis and measurements of landscape properties

Alkalinity was determined through acid-neutralizing capacity. The pCO_2 was calculated from the pH and alkalinity with corrections for temperature and air pressure (Cole et al., 1994; Weiss, 1974). A mean atmospheric CO_2 concentration of 390 ppm was adopted as the average atmospheric concentration, to determine whether the water was undersaturated ($pCO_2 < 390$ µatm), supersaturated ($pCO_2 > 390$ µatm) or

Table 2
Description of the main environmental variables used in the analyses. For more methodological details of these and additional variables, see Methods (Section 2.3) and Supplementary material (Appendix A – Section II).

Category	Variable	Units	Rationale (reference)	SOURCE	Measurement method
Response variable	Partial pressure of carbon dioxide (pCO_2)	µatm	Integrative ecosystem variable that reflects multiple processes. Provides information about the degree of carbon saturation in the water (Jonsson et al., 2003).	Our survey	Calculated from pH and alkalinity with corrections for temperature and air pressure (Cole et al., 1994; Weiss, 1974).
Trophic state	Chlorophyll-*a* (Chl-*a*)	µg L^{-1}	Proxy of phytoplankton primary production which may decrease water pCO_2 through the incorporation of CO_2 into organic matter (Williamson et al., 2009) and their catabolic processes that release CO_2 (Cole et al., 1994; Jonsson et al., 2001).	Our survey	Pigments extracted from filters with 95% ethanol and absorbance measured at wavelengths 665 and 750 nm (Jespersen and Christoffersen, 1987).
	Total nitrogen (TN)	mg L^{-1}	Important limiting nutrient for autotrophic and heterotrophic production in freshwater ecosystems (Elser et al., 1990).	Our survey	Total Carbon Analyzer coupled with the TN analyzer module (TOC-VPN; Shimadzu).
	Total phosphorus (TP)	mg L^{-1}	Important limiting nutrient for autotrophic and heterotrophic production in freshwater ecosystems (Elser et al., 1990), especially in the eutrophic semi-arid reservoirs, which are dominated by nitrogen-fixing cyanobacteria.	Our survey	After oxidation of organic phosphate compounds using persulfate (Valderrama, 1981) and estimated as the soluble P (Murphy and Riley, 1962).
	Dissolved organic carbon (DOC)	mg L^{-1}	Commonly an important predictor of pCO_2 in lentic ecosystems (Larsen et al., 2011).	Our survey	Total Carbon Analyzer coupled with the TN analyzer module (TOC-VPN; Shimadzu).
	Planktonic community respiration rates (PR)	µg C L^{-1} h^{-1}	Usually contributes to the increase of pCO_2 in the water (Carignan et al., 2000).	Our survey	Difference between initial and final O2 concentrations divided by the incubation time (Briand et al., 2004).
Carbon allocthony	Soil organic carbon (SOC)	Kg C m^{-2}	Proxy for the amount of terrestrial OC in catchments potentially entering inland waters (Drake et al., 2017)	Atlas of the Biosphere	Tabulate Area tool in ArcMap 10.5.1.
	SUVA254	L mg C^{-1} m^{-1}	Index of the aromaticity of DOC, with values higher than 4 L mgC–1 m–1 indicating the presence of more complex aromatic moieties, and values below 3 L mgC–1 m–1 indicating the dominance of hydrophobic microbial-dominated compounds (Weishaar et al., 2003).	Our survey	The UV absorbance at k = 254 nm (A250) normalized to the corresponding DOC concentration (Lambert et al., 2015).
	a250:a365 ratio	Ratio	Indicator of the relative size of organic molecules (Strome and Miller, 1978). The higher the ratio, the lower the aromaticity and the smaller the relative molecular size	Our survey	
Lake morphometry	Depth	m	Affects the proportion of the depth of the euphotic zone to the lake depth, and the contribution of sediment respiration to the water column, especially in small shallow systems (Kortelainen et al., 2006).	Our survey	Calibrated anchor line
	Lake surface area (LA)	km^2	Determines the extent of water-atmosphere interface that can affect the strength of CO2 influx/efflux (Prairie et al., 2002)	TOPODATA	Lake and reservoir polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2016).
Landscape properties	Catchment surface area (CA)	km^2	Contributes to the amount and heterogeneity of terrestrial carbon and nutrient inputs to inland waters (Knoll et al., 2013)	TOPODATA	Lake and reservoir polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2016).
	Land use Forested Anthropogenic	km^2	May affect the input of terrestrial carbon and nutrients to inland waters (Knoll et al., 2013). May reduce nutrient input, leading to decreasing trophic states May increase nutrient input, thereby increasing eutrophication	MapBiomas Initiative	Land-use classification for Caatinga and Atlantic Forest biomes (Forests = Fo, Natural non-forest = Nf, Agriculture/Pasture = Ag, Urban/Developed lands = Ur. Agriculture/Pasture and Urban/Developed use were grouped into Anthropogenic use (Ant) since these types of land use have generally similar effects on the increase of allochthonous nutrient input to waterbodies (Foley et al., 2005).
Hydrology	Precipitation	mm	Affects the runoff strength of terrestrial C inputs to inland waters via subsurface and groundwater flow. Also increases volume and in turn reduces pCO_2 in the water (Cole et al., 2007; Marotta et al., 2010).	INMET	Spatial dataset - cumulative for years (from January 2012 to September 2012); Seasonal dataset - monthly cumulative precipitation.
	Volume	m^3	Decreases the relative importance of ecosystem processes at benthic-pelagic and land-water interfaces to the water pCO_2 (Prairie et al., 2002; Schindler and Scheuerell, 2002).	Our survey and EMPARN	Hyperbolic function 0.43 × Lake area × Depth (Post et al., 2000)

in equilibrium with the atmosphere (pCO_2 ~ 390 μatm). We used 12 in-lake, 3 hydrological, 3 lake morphometric and 5 landscape property variables. For detailed description of the methods adopted to determine all 22 variables used in this study, please refer to the supplementary material (Appendix A). A summary of the methodological procedures used to determine the main variables of this study is provided in Table 2.

The aquatic ecosystems were classified into trophic status, as oligotrophic, mesotrophic, eutrophic and hypereutrophic, from the less productive to the most productive. This classification can be based in several environmental parameters, but mainly in the chlorophyll-a concentration, as a response of primary production processes in the water column. However, the classification levels can shift in Ecosystems from different characteristics, such as depth and climate conditions. As our dataset comprise tropical shallow ecosystems from a humid to a semi-arid area, we adopted a probabilistic distribution of the trophic status of Salas and Martino (1990) for the humid and sub-humid ecosystems and more specifically, the Thornton and Rast (1993) classification for the semi-arid ecosystems.

2.4. Data analysis

It was recently demonstrated that pCO_2 estimated from alkalinity measurements in organic-rich, acidic and highly alkaline waters might be largely overestimated (Abril et al., 2015). Thus, to avoid biased conclusions based on results obtained because of this methodological artifact, we also included filtered subsets of data. We filtered the 102-ecosystem pCO_2 dataset, excluding all systems with total alkalinity lower than 1 mmol L^{-1}, which reduced the sampling size of the spatial ($n = 44$ ecosystems; high-alkalinity spatial subset) and seasonal ($n = 102$ samplings; high-alkalinity seasonal subset) datasets (Fig. S2). This criterion excluded most of the humid coastal lakes such as Bonfim, which had very low alkalinity. We also removed Riacho da Cruz Lake (ID = 67) from the dataset because it showed extreme values in many variables and was therefore considered a multivariate outlier. We used a Kruskal-Wallis test followed by post-hoc Dunn's test to compare our pCO_2 data against a broad worldwide pCO_2 dataset (Sobek et al., 2003; Kosten et al., 2010; Raymond et al., 2013; Borges et al., 2014; Pinho et al., 2016) for systems with pH higher than 6.5 ($n = 17{,}086$) including different latitudinal regions, and also against a Brazilian dataset including lentic ecosystems from different biomes ($n = 421$).

The rationale for the selection of variables is described in Table 2. Variables (except for pH) were log-transformed to meet normality and homoscedasticity requisites of the statistical analysis. First, we used linear models to evaluate the main and summed effects of the abiotic and biotic in-lake variables, hydrology (volume and precipitation) and landscape properties (Table 2) on the pCO_2 spatial and seasonal variability, using the *lm* function of the package 'nlme' (Pinheiro et al., 2018) in R Statistical Software (version 3.4.2, <www.r-project.org>). We built models containing all variables and used the function *aictab* in the 'Aiccmodavg' package to identify the best-fitting models (Mazerolle, 2017). This selection procedure retains the best-predicting model by balancing the number of variables and the explanatory power added to the model (Burnham and Anderson, 2002). We used the small-sample-size corrected version of the Akaike information criterion (AICc) for the temporal subsets. Best-predicting models were those that had the smallest AICc scores (Burnham and Anderson, 2002). Differences in AICc values (ΔAICc) <2 indicate substantial evidence for the validity of alternative models, ΔAICc values between 3 and 9 indicate that alternative models have considerably less support, and ΔAICc >10 indicates that alternative models are highly unlikely to be valid (Burnham and Anderson, 2002).

We used linear mixed-effects models to evaluate individual and interactive effects of the factors "system" (Gargalheiras, Cruzeta and Extremoz) and "season" (dry and rainy) on the response variable pCO_2 using the *lmer* function of the package 'lme4' (Bates et al., 2015). Sampling station was considered as a random effect, to avoid problems associated with multiple pairwise testing (Bolker et al., 2009).

With respect to the spatial dataset, we applied a structural equation model (SEM) to further investigate the influences of environmental factors on the pCO_2. To reduce the number of variables entering the SEM, we performed a Principal Components Analysis (PCA) based on a correlation matrix of environmental variables (standardized with the *decostand* funtion in R), using the function *prcomp* of the package 'kazaan'. The first two axes (PC1 and PC2) were significant ($p < 0.05$, Monte Carlo test) and explained 59% of the data variation. The PC1 was clearly related to the trophic state (chl-*a*, TP, TN, DOC, PR, Secchi disk depth), explaining 38.8%, while the PC2 was related to the C allochthony (SOC, $SUVA_{254}$, a350:a365) and explained 20.2% of the variance (Fig. S3). The scores of the components PC1 and PC2 were extracted and used in the SEM as integrative variables representative of "trophic state" and "C allochthony".

Finally, we used SEM to test the direct and indirect effects of land use (forested and anthropogenic area), volume, trophic state (PC1 scores) and C allochthony (PC2 scores) on the water pCO_2. SEM is a statistical procedure used to establish the direct and indirect effects among multiple variables, as well as to evaluate possible covariances between them (Pires et al., 2016; Domingues et al., 2017). This approach allows weighing the effect of multiple causal factors on several response variables, using an integrative perspective. All regressions between variables in our model were established based on (a) the potential relationships previously observed with the simple and multiple regressions and (b) the expected effects based on the literature. The goodness-of-fit of the model was tested using a Chi-square test and Bollen-Stine bootstrap, due to the small sample size ($n = 43$; Bollen and Stine, 1992). A non-significant chi-square test indicates that there is no deviation between the observed covariance matrix and the proposed model in SEM, and the model is considered acceptable. We used the following indexes to decide if the model showed a good fit: (i) a Root Mean Square Error of Approximation (RMSEA) equal to or higher than 0.07 (Steiger, 2007); (ii) Standardized Root Mean Square Residual (SRMR) <0.05; (iii) Comparative Fit Index (CFI) equal to or higher than 0.96; and (iv) Tucker-Lewis Index (TLI) equal to or lower than 0.96 (Hu and Bentler, 1999). The SEM analysis was performed with the 'lavaan' package (Rosseel, 2012). All scripts and original data used for the figures and analysis are provided at: https://github.com/pcjunger/pCO2_RN_ms.

3. Results

3.1. Spatial dataset

We found high variability of pCO_2 among the aquatic ecosystems (Coefficient of variance = 1.26), with pCO_2 levels ranging from 28 to 21,710 μatm. The systems also varied widely in their physical, chemical and biological characteristics (Fig. 2A; Table S1). Most systems showed hypereutrophic (51%) and eutrophic (18.6%) conditions. Mesotrophic conditions were found in 24.7% of the systems, while oligotrophic conditions comprised 5.9% of the systems (full dataset; Fig. 3). Overall, 92% of the ecosystems were CO_2-supersaturated and 8% were CO_2-undersaturated (full dataset; Fig. 3). The oligotrophic systems ($n = 6$) were all CO_2-supersaturated, as were most of the mesotrophic systems ($n = 25$; 92% supersaturated, with only two systems (8%) undersaturated with CO_2). The share of undersaturation was not much higher in the hypereutrophic and eutrophic ecosystems ($n = 71$; 91% CO_2-supersaturated and six systems (9%) undersaturated). Most of the afternoon samples were CO_2-supersaturated (88%), demonstrating that these systems were supersaturated regardless of the time of day (full dataset; Fig. S4). There was no significant difference (*t*-test; $p > 0.05$) between reservoirs and lakes, nor between humid and semi-arid systems for pCO_2 levels (high-alkalinity spatial subset; Fig. S5).

The range of pCO_2 in these systems (9–40,020 μatm) was within that found in tropical ecosystems (1.5–40,497 μatm) and similar to the range

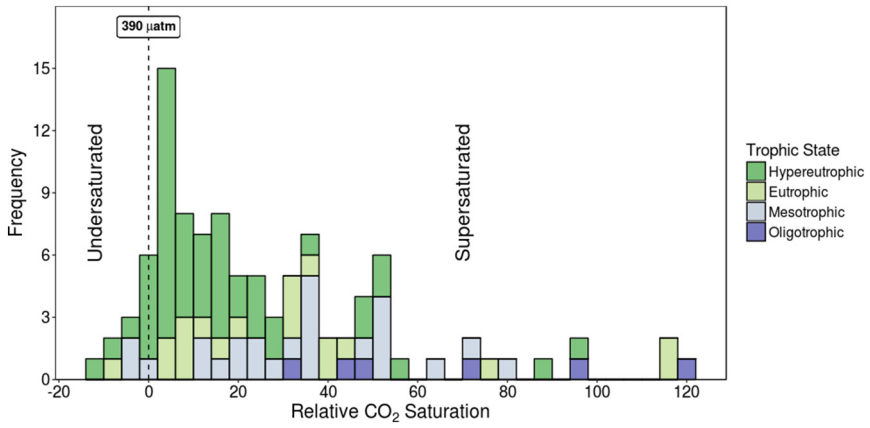

Fig. 3. Histogram showing the CO_2 saturation distribution for the 102 aquatic systems sampled (full spatial dataset) categorized according to their trophic state. The dashed line represents the atmospheric balance at 390 µatm, which divides the CO_2 supersaturated ecosystems to the right and the CO_2 undersaturated ecosystems to the left.

in subtropical (28–27,761 µatm) ecosystems (Fig. 4A). Higher pCO_2 values ($p < 0.005$) were recorded in this study compared to pCO_2 from high-latitude (Temperate, Subpolar and Polar) systems (Fig. 4A). The mean pCO_2 in our study was 2.8, 2.2 and 4.5 times higher than the mean pCO_2 in temperate, subpolar and polar ecosystems, respectively (Fig. 4A). The pCO_2 values recorded here in the semi-arid regions (Caatinga Biome) were significantly ($p < 0.005$) lower than those in the Amazon Rainforest, Pantanal floodplain and Atlantic Forest, respectively (Fig. 4B).

Linear regression-model analyses revealed that the pCO_2 was significantly related to the concentrations of chl-*a*, DOC and dissolved oxygen (all negatively correlated), and was positively correlated with both ecosystem volume and surface area (Figs. S6, S7 and S8; for a detailed description of these results see Suppl. Material). In addition, according to multiple-regression models, SOC, DOC and chl-*a* were the most important explanatory variables for pCO_2 in the spatial dataset (Table S4; see Suppl. material).

The SEM analysis indicated no significant deviation between the observed co-variance matrix and the predicted model ($\chi 2 = 2.55$; df = 4; $p = 0.64$; AIC = 470.2). The model also showed good-fit indexes (CFI = 1.0, TLI = 1.17, SRMR = 0.03; Fig. 5). The SEM results showed that the water volume had a negative effect on the trophic state ($r = -0.63$), and an indirect positive effect on pCO_2, through the variation in the trophic state ($r = 0.4$; Fig. 5). Both types of land use (km^2) had strong effects on the trophic state: anthropogenic area was positively related ($r = 0.97$), while forested area was negatively related to trophic state ($r = -0.92$; Fig. 5).

3.2. Seasonal dataset

We found high variability of pCO_2 in the seasonal dataset (CV = 191%), with pCO_2 levels ranging from 11 to 40,020 µatm. We also observed wide variations in several environmental variables in the seasonal dataset including the four systems (Fig. 2B; Table S2). The seasonal dataset ($n = 141$) was comprised mostly (72%) of observations of CO_2 supersaturation. Of a total of 39 samples with CO_2-undersaturation conditions (28%), most (82%) were found in the hypereutrophic ecosystems (Gargalheiras and Cruzeta). In Gargalheiras Reservoir, we recorded approximately equal frequencies of undersaturated (55%) and supersaturated (45%) conditions. Samples from Cruzeta Reservoir were mostly supersaturated (76%), but on nine occasions (24%) were CO_2-undersaturated. Extremoz Reservoir and Bonfim Lake had 92% and 86% CO_2-supersaturated samples, respectively.

We recorded a negative relationship between pCO_2 and chl-*a* using the seasonal dataset (Fig. S6). We also found that pCO_2 was negatively linked to dissolved oxygen, using the complete seasonal dataset (Fig. S7). The negative relationship between pCO_2 and dissolved oxygen was driven mainly by the semi-arid reservoirs (Fig. S7).

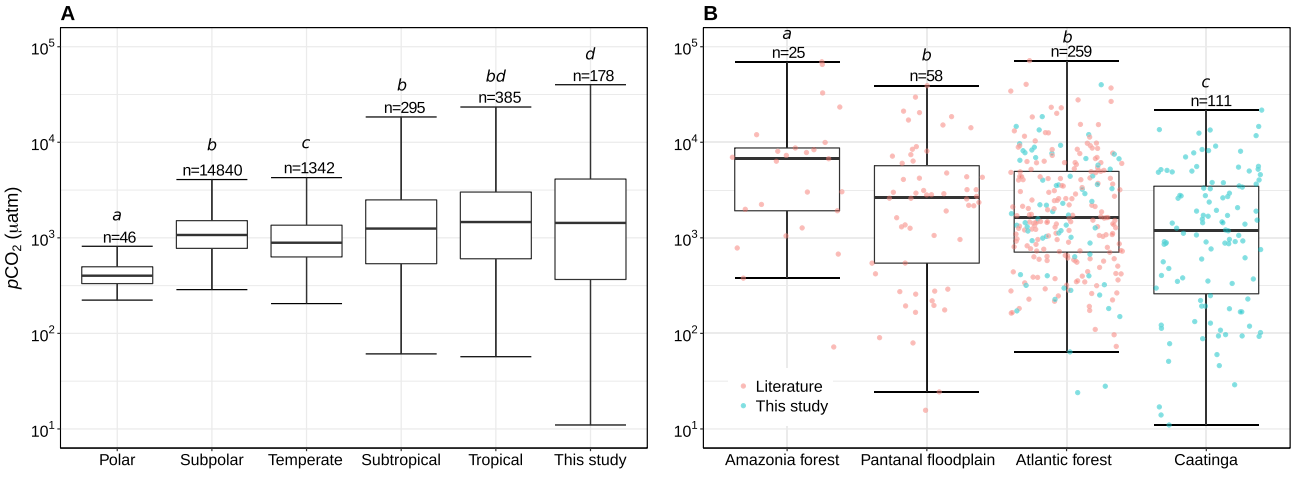

Fig. 4. Comparison of the pCO_2 of this study with published values (A) in different climate regions, defined by latitudes (Polar: >70°; Subpolar: 56–70°; Cold temperate: 34–56°; Subtropical: 20–34°; Tropical: 0–20°) and (B) the different Brazilian biomes, contrasted with the semi-arid Caatinga data of our study. The literature data (pH > 6.5) were obtained from Sobek et al., 2005, Kosten et al., 2010, Raymond et al., 2013, Borges et al., 2014 and Pinho et al., 2016. Total observations (n) after filtering (pH > 6.5) were $n = 17,086$ and 421 for the global and the Brazilian databases, respectively. Significant differences are represented by the letters a, b, c, d ($p < 0.001$). Fig. A was adapted from Sobek et al., 2005.

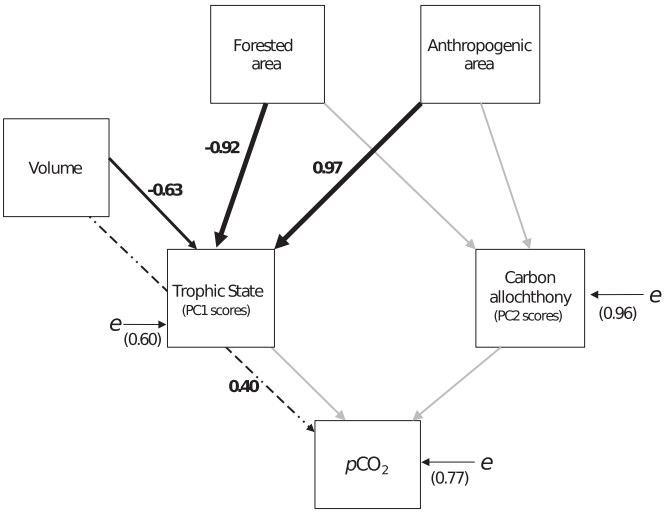

Fig. 5. Direct and indirect effects of land use, trophic state, carbon allochthony and water volume on pCO_2, as determined by the structure equation model ($\chi^2 = 2.55$; df = 4; $p = 0.64$; AIC = 470.20; SRMR = 0.03; CF1 = 1.0; TLI = 1.174). Significant effects ($p < 0.05$) are represented as black arrows, while nonsignificant effects are represented as gray arrows. Direct effects are represented as solid arrows and indirect effects are represented as dashed arrows. Values above each arrow are the standardized coefficient estimates for each significant link. The arrow thickness is proportional to the coefficient estimate. *e* = standard errors.

Precipitation, volume and chl-*a* proved to be the best explanatory variables for pCO_2 in Gargalheiras (Table 3). These variables explained 33% of the pCO_2 seasonal variability and comprised the best-fitting model to seasonally describe pCO_2 in this semi-arid reservoir (Table 3). Precipitation ($\rho = 0.34$) and water volume ($\rho = 3.83$) had a positive impact on pCO_2, and chl-*a* ($\rho = -0.62$) had a negative effect. Precipitation and bacterioplankton respiration (BR) constituted the most parsimonious model describing the pCO_2 seasonal variability in Cruzeta (Table 3). The combination of these variables explained ~47% of the pCO_2 seasonal variability, with both precipitation ($\rho = 0.39$) and BR ($\rho = 1.50$) having a positive effect on pCO_2 in this semi-arid reservoir (Table 3). Precipitation ($\rho = 0.28$) alone was the most important driver of pCO_2, explaining almost 20% of the seasonal variability in Extremoz Reservoir (Table 3). Adding chl-*a* or DOC to the model reduced the explanatory power of the model to around 16% (Table 3). The Zeu:depth ratio ($\rho = 3.52$) and DOC ($\rho = 2.98$) together represented the best-fitting model, explaining 16% of the pCO_2 seasonal variability in Bonfim coastal lake (Table 3).

In Gargalheiras, Cruzeta and Extremoz, pCO_2 was significantly higher in the rainy season than in the dry season (Fig. 6A; Table 4). No seasonal effect on pCO_2 in Bonfim Lake was found (Fig. 6A). pCO_2 levels differed significantly among the reservoirs (Table 4), although seasonality explained a higher proportion of variance in pCO_2 ($F = 16.67$) than the factor "reservoir" ($F = 13.68$) (Table 4). On average, pCO_2 was higher in Extremoz ($p < 0.0001$) and Cruzeta ($p < 0.05$) than in Gargalheiras (Fig. 6A). Differences in pCO_2 among the three sampling stations were significant (Fig. 6A) in Gargalheiras, where the inflow sampling station (P3) showed levels fourfold higher than the others, particularly during the rainy season (Fig. 6A). Seasonal patterns of pCO_2 were further investigated by exploring the relationships between delta volume (monthly differences) and precipitation and pCO_2 in each lake (Fig. 6B). Delta volume had a significant positive relationship with rainfall in Gargalheiras, Cruzeta and Extremoz, but not in Bonfim (Fig. 6B). There was a trend of increasing pCO_2 with increasing precipitation in the reservoirs, but not in the coastal Bonfim Lake (Table 4; Fig. 6B and Fig. S1).

4. Discussion

We found a consistent prevalence of CO_2 supersaturation in these low-latitude lakes and reservoirs (mainly those in the semi-arid region), in both space and time, which is consistent with our working hypothesis. Analysis of the spatial dataset showed that the trophic state was affected by the forested and anthropogenically impacted areas of catchments, although we did not find an effect of land use on pCO_2. On the other hand, water volume had a negative effect on the trophic state, which mediated a positive indirect effect on pCO_2. In the temporal approach, we found that chl-*a* was negatively linked to pCO_2, but pCO_2 was supersaturated even in systems with high phytoplankton densities, indicating the importance of external C inputs. Our results demonstrated that precipitation drives the pCO_2 seasonal variability in these ecosystems: higher pCO_2 during the rainy season (diluting phytoplankton and potentially increasing allochthonous inputs from the catchment) and lower pCO_2 in the dry season (still mostly supersaturated), due to the higher primary production in response to increasing nutrient concentrations in lower water volumes. Here we discuss our results in the global and regional contexts, specifically how the regional climate directly and indirectly affects the CO_2 dynamics and the prevalence of CO_2 supersaturation in highly productive ecosystems.

4.1. Prevalence of CO_2 supersaturation despite predominantly eutrophic conditions

Most of the ecosystems were supersaturated with CO_2, even though they were mostly hypereutrophic or eutrophic (Fig. 3), which agrees with our hypothesis but contradicts many previous studies that found that higher primary production resulted in net CO_2 uptake (Finlay et al., 2010; Balmer and Downing, 2011; Gu et al., 2011; Pacheco et al., 2014). Recent investigations, although with very limited datasets, have also found that eutrophic reservoirs located in the same semi-

Table 3
Best-fitting regression models describing pCO_2 using the seasonal subset (N = 102) divided by each ecosystem: Gargalheiras (n = 42), Cruzeta (n = 42), Extremoz (n = 26) and Bonfim (n = 42). Precip: monthly cumulative precipitation; Vol: water volume; Chl-*a*: chlorophyll-*a*; BR: bacterial respiration; DOC: dissolved organic carbon; Zeu: depth of the euphotic zone. AICc = Akaike information criterion for small samples; R^2 = Adjusted R-squared. *P*-values in bold represent significant relationships.

Ecosystem	Model	AICc	Δ AICc	R^2	*p*-Value
Gargalheiras	$log_{10}\,pCO_2 = -25.69 + (0.34 * log_{10}\,\text{Precip}) + (3.83 * log_{10}\,\text{Vol}) - (0.62 * log_{10}\,\text{Chl-}a)$	75.02	**0**	0.329	<**0.0005**
	$log_{10}\,pCO_2 = -18.29 - (0.79 * log_{10}\,\text{Depth}) + (2.99 * log_{10}\,\text{Vol}) - (0.53 * log_{10}\,\text{Chl-}a)$	77.45	**2.44**	0.289	<**0.005**
	$log_{10}\,pCO_2 = -18.96 + (3.03 * log_{10}\,\text{Vol}) - (0.78 * log_{10}\,\text{Chl-}a)$	79.17	4.15	0.233	<**0.005**
Cruzeta	$log_{10}\,pCO_2 = 0.28 + (0.39 * log_{10}\,\text{Precip}) + (1.50 * log_{10}\,\text{BR})$	44.38	**0**	0.468	<**0.0005**
	$log_{10}\,pCO_2 = 0.83 + (0.38 * log_{10}\,\text{Precip}) + (1.52 * log_{10}\,\text{BR}) - (0.38 * log_{10}\,\text{Chl-}a)$	45.21	**0.83**	0.487	<**0.0005**
	$log_{10}\,pCO_2 = -2.99 + (0.37 * log_{10}\,\text{Precip}) + (0.56 * log_{10}\,\text{Vol}) + (1.43 * log_{10}\,\text{BR}) - (0.47 * log_{10}\,\text{Chl-}a)$	47.80	**3.41**	0.477	<**0.005**
	$log_{10}\,pCO_2 = 0.84 + (0.37 * log_{10}\,\text{Precip}) - (0.30 * log_{10}\,\text{Depth}) + (1.58 * log_{10}\,\text{BR}) - (0.29 * log_{10}\,\text{Chl-}a)$	48.17	**3.79**	0.470	<**0.005**
Extremoz	$log_{10}\,pCO_2 = 2.99 + (0.28 * log_{10}\,\text{Precip})$	38.49	**0**	0.194	<**0.05**
	$log_{10}\,pCO_2 = 3.07 + (0.31 * log_{10}\,\text{Precip}) - (0.15 * log_{10}\,\text{Chl-}a)$	41.25	**2.76**	0.161	=**0.05**
	$log_{10}\,pCO_2 = 2.99 + (0.28 * log_{10}\,\text{Precip}) - (0.03 * log_{10}\,\text{DOC})$	41.34	**2.85**	0.158	=**0.05**
Bonfim	$log_{10}\,pCO_2 = 3.32 + (3.52 * log_{10}\,\text{Zeu:depth}) + (2.98 * log_{10}\,\text{DOC})$	88.64	**0**	0.167	<**0.05**
	$log_{10}\,pCO_2 = 3.69 + (3.77 * log_{10}\,\text{Zeu:depth})$	91.07	**3.41**	0.115	<**0.05**
	$log_{10}\,pCO_2 = 3.05 + (3.53 * log_{10}\,\text{DOC})$	92.25	**3.79**	0.068	=**0.06**

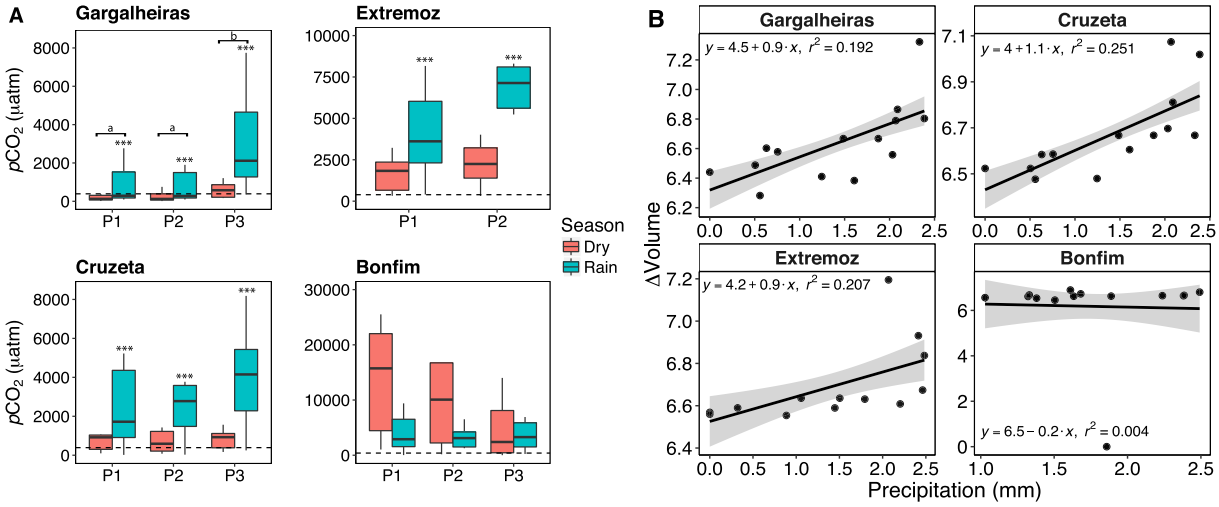

Fig. 6. (A) Independent and interactive effects (mean ± 1 SE) of seasonality and sampling stations on pCO_2 for each ecosystem. Terms in the legend: "Dry" = sampled in the dry season; "Rain" = sampled in the rainy season. The asterisks (***) represent significant differences in the mean values of pCO_2 between seasons ($p < 0.05$) at each sampling station. Different letters above brackets depict statistical differences in the mean values of pCO_2 among the sampling stations, irrespective of seasonality ($p < 0.05$). The horizontal dashed line indicates the atmospheric CO_2 concentration (390 µatm). (B) Water volume variation in response to rainfall (values are log_{10}-transformed). Linear regressions were significant ($p < 0.05$) in all reservoirs, except for Bonfim lake.

arid region as this study are mostly CO_2-supersaturated (Mendonça Júnior et al., 2018) and emit large amounts of C (CO_2 and CH_4) to the atmosphere (Almeida et al., 2016). It has been consistently shown that inland water bodies at lower latitudes were CO_2-supersaturated (Marotta et al., 2009a, 2009b; Kosten et al., 2010). In agreement, the average pCO_2 in the current study was higher than those at higher latitudes (Fig. 4A). On the other hand, the eutrophic semi-arid ecosystems in the Caatinga Biome showed the lowest pCO_2 values compared to ecosystems in other Brazilian biomes (Pantanal floodplain, Amazon and Atlantic forests) (Fig. 4B). This observation illustrates not only the role of eutrophication in reducing the water pCO_2 in tropical inland waters, but also the high contribution of terrestrial C inputs to aquatic systems in biomass-rich ecosystems such as the Pantanal and the Amazon, compared to drier and SOC-poorer biomes such as the Caatinga (Menezes et al., 2012).

Several potential mechanisms may account for the prevalence of CO_2 supersaturation over time and space in these systems, regardless of the trophic state: (A) the perennial high temperatures at these low latitudes (Fig. 2; Tables S1 and S2) support high respiration rates, i.e. low growth efficiency in the plankton community (Brown et al., 2004; Yvon-Durocher et al., 2010; Amado et al., 2013; Kraemer et al., 2017); (B) the higher incidence of solar radiation in low-latitude ecosystems both increase DOM photochemical degradation and decrease bacterial growth efficiency, which results in high CO_2 release through high BR rates (Amado et al., 2013, 2015), as recorded here (Fig. 2; Tables S1 and S2); (C) the less efficient C burial in warmer shallow ecosystems where sediment respiration contributes more to the whole-ecosystem CO_2 balance (Kortelainen et al., 2006; Flanagan and McCauley, 2008; Cardoso et al., 2014; Mendonça et al., 2014; Almeida et al., 2016), as suggested here by the high pCO_2 levels near the bottom of Gargalheiras and Cruzeta reservoirs (Fig. S10 and S11), indicating that sediment respiration is likely an important CO_2 source in these systems. Similarly, in a small eutrophic semi-arid reservoir (ESEC reservoir, available in our spatial dataset [Lake ID = 43]), massive sediment respiration exceeded the high primary production (Almeida et al., 2016); and (D) precipitation-driven C input from the catchment may also be an important source for CO_2 saturation in these low-latitude systems, as demonstrated in other regions (Weyhenmeyer et al., 2015; Wilkinson et al., 2016; Amaral et al., 2018), since we recorded higher pCO_2 values during the rainy season (Fig. 6A).

Table 4
Summary of the general linear mixed-models (GLMM) of the analysis of variance for the effects of seasonality (dry and rainy seasons), reservoirs (Gargalheiras, Cruzeta and Extremoz) and their interactions on water pCO_2. Sampling stations were considered as a random factor. Bold *P*-values indicate a statistically significant effect ($p < 0.05$).

Factors	df	F	*p*-Value
pCO_2			
Seasonality (S)	1	16.67	**0.00009**
Reservoir (R)	2	13.68	**0.000006**
S × R	2	0.09	0.92
Error	90		

4.2. Effects of phytoplankton biomass oscillations on CO_2 saturation through changes in water volume

Phytoplankton seems to play an important role in the C balance in these ecosystems. Usually in lakes, chl-*a* and pCO_2 are negatively related, since primary production is fueled by CO_2 and removes it from the water (Jansson et al., 2008; Urabe et al., 2011). Thus, the trophic state of an aquatic ecosystem should directly affect the pCO_2 dynamics. We found here that the fluctuations in water volume directly affected the trophic state of the ecosystems, thereby indirectly affecting pCO_2 (Fig. 5). Lower water volume concentrated nutrients, thereby leading to increasing eutrophication and decreasing pCO_2. Contrariwise, an increase in water volume diluted nutrients and phytoplankton biomass, thereby decreasing eutrophication (Figs. 5 and 6 and S1 and S6). This mechanism is in line with our hypothesis and has been described recently for a subtropical lake (Tonetta et al., 2017) and for eutrophic reservoirs in the semi-arid region of this study (Mendonça Júnior et al., 2018). It is important to highlight that the spatial samplings were here performed at the beginning of the dry period during an extremely dry year (Costa et al., 2016) and, at least for the semi-arid systems, there was no significant water input for several months. Therefore, in our spatial approach the water volume could also represent a proxy of residence time affecting nutrients processing by increasing the recycled primary production (i.e. primary production taking up nutrients that were released from recycling organic matter; They et al., 2017). The only exception in our seasonal survey was Bonfim Lake, with hydrological (not driven by precipitation) and CO_2 dynamics that clearly differed from the semi-arid and sub-humid reservoirs (Fig. 6; Table 3). The lack of a direct link between water volume and precipitation in Bonfim Lake can be explained by the groundwater inflow, which is independent of the seasonal precipitation patterns in the sandy catchments of these coastal lakes (Cunha et al., 1990). Further, this lake serves as a water

source for some neighboring municipalities, which may mask the natural seasonal variation of the water volume.

Interestingly, our spatial dataset also showed that pCO_2 is inversely linked to DOC (Fig. S9), which is contrary to expectations since DOC is often one of the main variables positively predicting pCO_2 in lakes (Larsen et al., 2011). This negative relationship can be explained by the large portion of DOC that is produced by algae (autochthonous production) in many of these productive systems (as substantiated by the positive relationship between DOC and chl-*a*; Fig. S9). This pattern is commonly observed in tropical ecosystems, because of the high production of phytoplankton exudates stimulated by high temperatures (Morana et al., 2014). Phytoplankton-excreted organic C can also be an important source of labile C for bacterial metabolism (Kritzberg et al., 2005; Farjalla et al., 2009), and therefore, abrupt mass die-offs or high excretion rates of phytoplankton blooms may fuel short-term increases in BR (Gudasz et al., 2012; Cardoso et al., 2013). Indeed, higher levels of pCO_2 occurred in systems with high rates of BR per unit of phytoplankton biomass (Fig. S9), indicating that bacterioplankton OC mineralization substantially supports CO_2 supersaturation in these systems (Freitas et al., 2018).

4.3. Precipitation as a link between the aquatic systems and their catchment

The high phytoplankton biomass was insufficient to drive the CO_2 below equilibrium concentration in these systems, which indicates the importance of external C sources to keep them predominantly CO_2-supersaturated, both spatially and temporally. Precipitation plays a major role in this process, through two main mechanisms, by transporting nutrients as well as organic matter and CO_2 from catchments to water bodies. Nonetheless, we found that pCO_2 was not related to C allochthony or precipitation in these systems, using the spatial approach (Fig. 5). This lack of relationship between these variables can be explained by (1) the buffering effect of the volume of the systems (which integrates morphological features such as size and depth), which is more important in explaining pCO_2 spatial variability (Fig. 5); or (2) the fact that our spatial sampling was conducted during the dry period of a very dry year (Costa et al., 2016), when volumes were much lower and the reservoirs were probably more dependent on internal processes (plankton activity and sediment respiration) than on allochthonous inputs (e.g. Thomaz et al., 2007; They et al., 2017). However, the higher levels of pCO_2 occurring during the rainy periods in the seasonal approach (Fig. 6) indicate the importance of terrestrial C inputs from the catchment (Drake et al., 2017) to support the high CO_2 concentrations in the water column, which might explain the associated error ($e = 0.77$) in the prediction of pCO_2 in the SEM using the spatial dataset (Fig. 5). This external support has been widely reported as a major supporter of CO_2 supersaturation in most aquatic ecosystems of the world (Weyhenmeyer et al., 2015; Wilkinson et al., 2016; Amaral et al., 2018), even those with extremely high primary production (Bogard and del Giorgio, 2016).

The stronger effect of seasonality than inter-spatial variation on pCO_2 (Table 4) shows that sampling over time is essential, particularly in the semi-arid aquatic systems because of the wide variability of rainfall (Fig. 6; Table 3). This finding agrees with Knoll et al. (2013), who demonstrated the importance of measuring CO_2 flux over both weather-event and annual scales. This approach is still rarely used, as most studies have focused mainly on CO_2 spatial variability (Knoll et al., 2013), even though seasonal variation in rainfall, temperature and light are usually important factors regulating aquatic metabolism (Marotta et al., 2009a; Karlsson et al., 2012). In low-latitude lakes and reservoirs, precipitation is clearly the most important climate factor, since light and temperature vary little over the year (Sarmento, 2012).

4.4. Catchment land-use affects trophic state but not water pCO_2

We did not find a significant relationship between catchment land use and pCO_2 (Fig. 5), partly contradicting our hypothesis that differences in land use would produce high spatial variations in pCO_2. Since pCO_2 is an integrative ecosystem variable that responds to multiple environmental variables, land use may simultaneously affect variables that are positive and negative drivers of pCO_2. For instance, land use may have counterbalancing effects on SOC and nutrient availability, thereby resulting in a neutral global effect on pCO_2. Direct land-use impacts on water pCO_2 may be difficult to capture via snapshot spatial observations, especially during years with exceptionally long dry periods when connectivity between aquatic ecosystems and their catchments is probably lower (Thomaz et al., 2007).

Few studies have compared lakes with contrasting catchment land uses (e.g., forested vs agricultural) and showed a trend toward higher CO_2 in lakes surrounded by forested areas and lower CO_2 in lakes inserted in agricultural landscapes (Knoll et al., 2013). To our knowledge, no published report has demonstrated direct relationships between land use and pCO_2 in lakes using large-scale spatial datasets. A single study demonstrated that CO_2 concentration in lakes was positively linked to the catchment productivity (Maberly et al., 2012; however, in this study the pCO_2 estimates were based on alkalinity and would not have passed our selection criteria described in the Methods section). Besides, another study with boreal lakes (rich in terrestrial humic organic matter) also failed to directly connect the pCO_2 in the water to land use in the watershed but showed relationship with DOC (which was mainly of terrestrial origin; Sobek et al., 2003). Conversely, recent studies have found direct relationships between CO_2 levels and land-use categories in riverine ecosystems in boreal, temperate and tropical regions (Bodmer et al., 2016; Borges et al., 2015, 2018). The results for lentic and lotic ecosystems may differ because rivers and streams are more closely connected to their catchments than are lakes and reservoirs, where internal processes may be more important (Gergel et al., 1999).

The land-use types in the catchment areas had direct and antagonistic effects on the systems' trophic state (Fig. 5). Catchment areas dominated by urban settlements, agricultural and pasturelands, which are common in the humid and semi-arid regions of this study, showed higher trophic states (Fig. 5). Indeed, agricultural or urban areas usually input nutrients into aquatic ecosystems, causing eutrophication (Carpenter et al., 1998; Vanni et al., 2011; Le Moal et al., 2019), which in turn can stimulate primary production and C sequestration (Balmer and Downing, 2011). However, in our study, higher trophic states in anthropogenic catchment areas did not affect the CO_2 saturation in the water (Fig. 5). In contrast, the systems in catchment areas dominated by native forests were generally less productive (Fig. 5) probably because these forests may function as filters, reducing the amount of limiting nutrients entering water bodies and preventing eutrophication (Vanni et al., 2005; Palviainen et al., 2014; Schelker et al., 2016). However, we did not find any direct or indirect impact of forested areas on CO_2 saturation in these systems, which contradicts our expectations (Sand-Jensen and Staehr, 2007; Knoll et al., 2013).

4.5. CO_2 saturation and environmental changes in low-latitudes

We suggest that precipitation is a major driver of spatial and seasonal changes in several external and internal processes that drive the pCO_2 variability in low-latitude lakes and reservoirs. This is particularly important in the context of environmental changes, since the low-latitude region studied here is predicted to undergo both an increase of 4 °C in temperature and changes in precipitation patterns, with a 40% reduction in rainfall and increases in the intensity, frequency and duration of droughts during the 21st century (Marengo et al., 2010; PBMC, 2014). These precipitation changes will reduce the volume of water bodies, thereby increasing their susceptibility to eutrophication and causing drastic changes in these systems (Brasil et al., 2016; Menezes et al., 2018). Our results suggest that these ongoing shifts in precipitation could also lead to potential changes in regional C cycling, with enhanced CO_2 absorption and decreased terrestrial C input in the

systems. Under the current extreme droughts, these eutrophic ecosystems may completely dry up, exposing large amounts of OM accumulated in the sediments to microbial and photo-degradation, producing high C emissions that must be included in regional C balance studies in the future (Kosten et al., 2018; Marcé et al., 2019).

5. Conclusions

We conclude that low-latitude lakes and reservoirs are predominantly CO_2-supersaturated (92%), regardless of their trophic state (69.6% of hypereutrophic and eutrophic systems) and the nature of the surrounding landscape. High phytoplankton biomass contributes to reduce the pCO_2 levels in surface waters, but it does not necessarily result in net CO_2 uptake in low-latitude water bodies. We also conclude that the predicted decrease in water volume is expected to indirectly decrease CO_2 saturation, which represents an important negative feedback in the context of climate change. Seasonal variations in pCO_2 in low-latitude sub-humid and semi-arid reservoirs are large, with much higher pCO_2 during the rainy period due to phytoplankton dilution and external CO_2 inflow. Taken together, these results lead to the main conclusion that precipitation is a major force driving pCO_2 spatial and seasonal variability in this region, through two main mechanisms: (1) by driving the variations in water volume and thereby diluting or concentrating nutrients, phytoplankton biomass and organic matter; and (2) by transporting nutrients as well as organic matter and CO_2 from catchments to water bodies. We expect the conceptual framework that emerged from this study to lead to further investigations toward broadening our understanding of C cycling in these globally understudied ecosystems.

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Appendix A. Supplementary data

Supplementary material is divided into five sections: (I) a list of the abbreviations used in the text, (II) detailed descriptions of methods, (III) additional results, (IV) additional figures and (V) additional tables cited throughout the manuscript. Supplementary data to this article can be found online at doi:https://doi.org/10.1016/j.scitotenv.2019.01.273.

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